

## Letter

# The way back: recovery of trees from drought and its implication for acclimation

Resilience is a key concept in ecology, describing the capacity of a system to resist a disturbance, recover from it and return to a stable state (Lloret *et al.*, 2011; Hodgson *et al.*, 2015; Ingrisch & Bahn, 2018; see Box 1). Whilst it is indisputable and a matter of intensive research (e.g. McDowell *et al.*, 2008; Meinzer *et al.*, 2009; Vicente-Serrano *et al.*, 2013) that ‘resistance’, i.e. the ability of individuals and ecosystems to persist and maintain their functioning during a disturbance, is a key aspect of resilience, the importance of ‘recovery’ after a disturbance event for resilience comes more and more into the focus of research (e.g. Brodribb & Cochard, 2009; Galiano *et al.*, 2011; Arend *et al.*, 2016; Hagedorn *et al.*, 2016). Only recently, Ingrisch & Bahn (2018) proposed an approach to quantify resilience by jointly considering the disturbance impact (and thus resistance) and the recovery rate after the disturbance. As many other authors before, they assumed that after a disturbance the system recovers to its initial state, but other definitions of resilience include the possibility that a system may reach a new stable-state after release from disturbance pressure (Gunderson, 2000). Regardless of how resilience is described, the recovery process is central to any definition of resilience, as it reflects the inherent forces that drive a system back to a stable state of function, whether this is the pre-disturbance system state or some alternative stable state.

It is often assumed that the rate of recovery determines the resistance to the next disturbance event and thus the long-term stability of an ecosystem (Tilman & Downing, 1994). Thus, slow recovery after stress has been mostly seen in the light of long-term and continued impairment of functioning. The non-instantaneous recovery of trees after a disturbance could, however, not only be due to lags in function because of the negative impacts of drought but also a sign of acclimation responses. For example, an increase in hydraulic safety at the expense of growth following a drought event might be considered as a long-term impairment when looking at growth only but as an acclimation when considering overall functioning and resistance to subsequent drought events. We explore here to what extent recovery trajectories after drought events are related to acclimation conveyed by ecological stress memory and propose strategies to disentangle post-drought acclimation from impairment.

## Duration of recovery from drought-induced disturbances depends on a variety of factors

Episodes of droughts are expected to further increase in frequency and severity in many regions of the world (e.g. IPCC, 2013;

Spinoni *et al.*, 2018), putting strong pressure on forests; global observations of drought-induced forest decline and tree mortality already show this pressure (Allen *et al.*, 2010; Hartmann *et al.*, 2018; Schuldt *et al.*, 2020). Severe drought limits primary metabolic processes and tree physiological functions, and can strongly affect the whole ecosystem functioning and the ecosystem services that forests provide (Ciais *et al.*, 2005; McDowell *et al.*, 2008; Anderegg *et al.*, 2016). Due to their long lifespan, trees must have evolved specific mechanisms to cope with recurrent droughts, that is, the ability to survive water limitation and recover from it. The recovery of trees from an incidence of drought may take days, weeks or even years, depending on the timing, duration and severity of the experienced stress, on tree ontogeny, height and social position, and taxonomic group (Hanson *et al.*, 2001; Anderegg *et al.*, 2015; Bennett *et al.*, 2015; Grote *et al.*, 2016). Ruehr *et al.* (2019) provided a conceptual framework of the relationship between stress intensity and recovery within one growing season. Whilst the effects of mild stress are fully and immediately reversible, higher stress levels are supposed to result in structural damage, causing recovery to be slow and dependent on regrowth of lost and damaged tissues. Moreover, a recent study of a global tree-ring database suggests that slow recovery is associated with higher

### Box 1 Definitions

**Acclimation** (also referred to as phenotypic plasticity): Reversible shifts in phenotype in response to environmental pressure/disturbance, resulting from active and passive responses. Acclimation can occur when an environmental pressure is present continuously or might be conveyed by past experience of an environmental pressure (ecological memory).

**Resistance**: The ability of individuals and ecosystems to persist and maintain their functioning during a disturbance. Resistance is measurable through the concurrent impact of a disturbance on response parameters (indicative of functions). The higher the resistance the lower the impact of a disturbance (Ingrisch & Bahn, 2018).

**Recovery**: The capacity of individuals and ecosystems to return to the undisturbed ecosystem state and functioning following a disturbance.

**Resilience**: The capacity of individuals and ecosystems to maintain their functioning in the face of disturbance. It is determined by both, the capacity to reduce the impact (resistance) of a disturbance and to recover from the impact (recovery) after the disturbance (Ingrisch & Bahn, 2018). Our definition is broader than other definitions of resilience such as the one given by Lloret *et al.* (2011). These authors define resilience solely as the capacity to reach pre-disturbance levels of functions.

**Ecological memory**: The capability of past experiences of an individual or community to influence future ecological responses, including resistance, resilience and recovery in response to environmental pressure.

**Priming**: The process through which organisms prepare their phenotype for an improved response to future stress (Hilker *et al.*, 2016). A first, priming stress event can induce ecological (stress) memory.

mortality risk in conifers, whereas no such trend was found in woody angiosperms (DeSoto *et al.*, 2020). It has also been shown that when drought events occur in close sequence (i.e. when a second event occurs before the system has fully recovered from the first) the overall drought impact and the total recovery time can increase (Mitchell *et al.*, 2016).

Duration of recovery also depends on the scale and complexity of the function examined. Whilst molecular functions and physiological processes might regain function within days to weeks (Bogeat-Triboulot *et al.*, 2007; Hagedorn *et al.*, 2016; Iovieno *et al.*, 2016; Volkman *et al.*, 2016), recovery times of more than 1 year have been observed for more integrating processes such as gross primary productivity (Schwalm *et al.*, 2017), tree growth (Huang *et al.*, 2018), or water-use efficiency (Monserud & Marshall, 2001). Legacies of up to 4 years with reduced radial growth have been detected, especially in dry ecosystems (Anderegg *et al.*, 2015). The issues of scaling and complexity require particular attention to fully understand the recovery process, but also to avoid misleading conclusions about the overall resilience and its consequences for trees in response to drought.

### Priming and stress memory might convey long-term acclimation after a drought stress event

Integrating processes such as tree growth not only rely on the coordination of molecular processes, cellular mechanisms, plant structure, and whole-plant functioning, but may also convey acclimation to prevailing or antecedent conditions. It is well known that acclimation or phenotypic plasticity can partially or even fully compensate detrimental impacts of drought and other stressors (Nicotra *et al.*, 2010). In most approaches that assess acclimation experimentally, however, the environmental factor of interest is changed to a new level at the beginning of an experiment and kept constant on that level to study acclimation reactions both in the short- (Hanson & Sharkey, 2001; Atkin & Tjoelker, 2003) and long-term (e.g. Rodríguez-Calcerrada *et al.*, 2011; Martin-StPaul *et al.*, 2013; Felsmann *et al.*, 2017). While such approaches are important to understand general mechanisms of acclimation, they do not fully reflect natural conditions, where stress (e.g. drought) events of a finite duration occur. It is not clear if such event-based stressors convey longer-term acclimation after the stress has ceased. Here, the subsequent recovery process that constitutes an important part of the tree's overall drought response might be involved in acclimation to future stress periods. In general, it is unclear whether the extreme droughts that occurred in 2003 and 2018 in Central Europe induced long-term acclimation, and increased resilience of trees during subsequent stress periods. Such a process is referred to as ecological (stress) memory (Walter *et al.*, 2011) and has been defined as a mechanism or different sets of mechanisms that let a plant react to direct environmental drivers not only determined by their genetic capacity but also by their experience of antecedent (stress) conditions (cf. Ogle *et al.*, 2015; Gessler *et al.*, 2017).

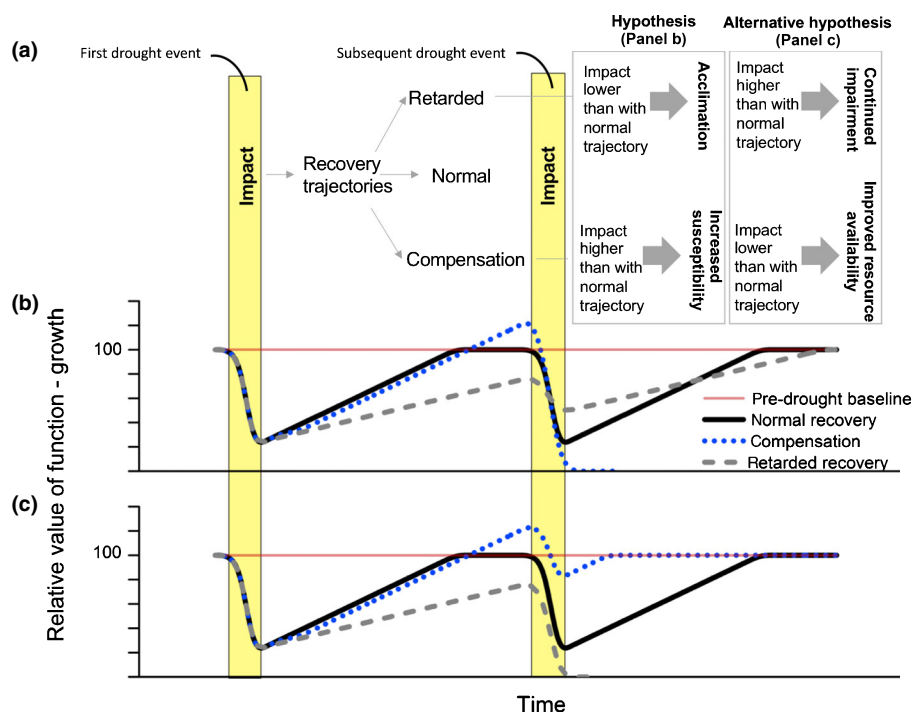
The process through which the phenotype of an organism gets adjusted for an improved response to future stress, and which thus induces stress memory, has been named priming (Hilker & Schmölling, 2019). The response of trees after a stress event – be it

growth or other functions – might thus be seen in the light of priming, acclimation and stress memory, and a delay in or failure to return to the initial state would not necessarily be considered damage or a reduction in vitality. Still, with respect to the framework of Ruehr *et al.* (2019) there might be stress intensity dependent threshold values: mild stress, that is fully compensated by stomatal closure and osmotic regulation and that will most likely not intensively affect growth and other central tree function might not be a priming event and thus not convey any acclimation in the longer-term. Stronger stress intensities, however, that activate repair mechanisms and induce strong changes in plant metabolism might do so. Finally, if a threshold of extremely severe stress is crossed, retarded or incomplete recovery might be mainly due to intensive loss and damage of tree tissues. However, it has been proposed that also mild stress can convey priming and stress memory (Hilker *et al.*, 2016) and thus deeper and more conceptual research on this topic is necessary.

### Slow recovery trajectories might reflect a controlled acclimation response optimizing survival in the long-term

In this regard, slow recovery, and thus low resilience in a classical sense (cf. Lloret *et al.*, 2011), with long-term legacies of reduced tree growth (recovery trajectory with retarded gain of function in Fig. 1) might be seen as structural acclimation under particular conditions. In fact, it has frequently been shown that the tree hydraulic system acclimates to drought by forming smaller xylem conduits (Corcuera *et al.*, 2004; Eilmann *et al.*, 2006, 2009; Arend & Fromm, 2007; Fonti *et al.*, 2013), which are thought to be less prone to hydraulic failure (Guet *et al.*, 2015) even though also higher hydraulic conductance together with higher cavitation vulnerability upon drought has been observed (Guérin *et al.*, 2020). As, however, the formation of smaller xylem conduits is negatively correlated with tree-ring width, growth limitations after a drought are not necessarily a sign of continuing vulnerability, but on the contrary would serve as a structural adjustment of the hydraulic system to increase drought tolerance. This would be in line with observations showing that slow-growing trees are less prone to hydraulic failure and mortality than fast-growing trees (Jansen *et al.*, 2013; Gessler *et al.*, 2018; Büntgen *et al.*, 2019).

Only recently, it has been shown that drought-induced growth reductions and wood anatomical adjustments come along with improved resistance to recurrent drought and less severe limitations of water and carbon balances (Tomasella *et al.*, 2019). In that sense, negative growth legacies could be considered as positive acclimation responses with respect to future drought events, thus optimizing a tree's survival in the long-term. Such a strategy in the years after drought would reduce short-term performance to optimize long-term survival as suggested by Galiano *et al.* (2017). In their work with seedlings, these authors showed that after drought release, prioritized incorporation of new assimilates into storage pools occurred rather than investment in growth even though other constraints on growth such as reduced hydraulic functions cannot be ruled out. Moreover, after the end of a drought period, preferential transport of new assimilates to the roots for the



**Fig. 1** Conceptual framework on how different recovery trajectories could affect the impact of a subsequent drought event (a) and depiction of different trajectories of recovery and hypothesized effects of repeated stress impact (b, c) on tree function such as radial growth. The yellow shaded areas in the four panels represent the exposure to a drought stress event. In (a) the hypothesis and the alternative hypothesis refer to the related panels (b) and (c), respectively. In (b) and (c) the black line shows a relatively fast recovery trajectory (normal recovery) with a recovery rate higher than that of the slow retarded recovery scenario (dashed grey line) after the first drought event. Moreover, a scenario with compensatory gain of function after stress release is shown (dotted blue line). In (b) and (c) two alternative scenarios for a subsequent (thus repeated) drought event directly after recovery (normal recovery), in the recovery phase (retarded slow recovery) or in the compensation phase (compensation) are shown. In (b) it is hypothesized that slow recovery conveys acclimation to a new drought event, whereas compensation increases susceptibility and eventually leads to mortality. In (c) retarded recovery is assumed to be a result of continued impairment of functions and thus reduces resistance to a new drought event, whereas compensation is assumed to be a result of competition release that improves resource availability during the subsequent drought event. For reasons of simplification, in both (b) and (c) the 'normal' recovery trajectory after the subsequent drought is assumed to be the same as after the first drought event (which is assumed to have not occurred directly after recovery).

re-establishment of root functioning and growth at the expense of the supply of aboveground tissues was observed (Hagedorn *et al.*, 2016). Strategies of increasing carbohydrate storage (O'Brien *et al.*, 2014) and prioritization of root compared to shoot growth (López *et al.*, 2009) are known to increase drought resistance in seedlings and can, thus, be also seen as an acclimation induced by an antecedent and no longer present extreme event.

### Fast recovery and post-drought compensation might make trees more susceptible to future droughts

In contrast to slow recovery and persisting growth depression, compensation of functioning after a drought (recovery trajectory with compensatory gain of function in Fig. 1), i.e. the increase of a function above the initial pre-drought value, has also been observed but has received little attention in the stress-ecological studies. Still, the phenomenon of compensatory growth is well established in agriculture, and while mainly applied to the field of plant-herbivore interaction (Orcutt & Nilsen, 2000), it is known that growth and photosynthesis may also increase after a drought. On the one hand, such post-drought compensation might reflect demographic effects, i.e. increased mortality rates during the stress

event and thus competition release for the surviving individuals (cf. Cavin *et al.*, 2013; Anderegg *et al.*, 2015; Huang *et al.*, 2018). On the other hand, it has also been shown to be independent of changes in competition and is assumed to be an inherent physiological mechanism (Spieß *et al.*, 2012; Arend *et al.*, 2016; Trugman *et al.*, 2018), as for example when the root and stem hydraulic system is overbuilt for the residual leaf area (Vanderklein & Reich, 1999). This mechanism might reduce the overall impact of drought by compensating for the losses after the stress event (Hagedorn *et al.*, 2016). It might be seen as a reaction that improves functioning over the longer-term to maintain or even increase a tree's competitive strength after a drought event. With respect to stem growth, compensation might be also a result of preferential carbon allocation to rebuild damaged xylem that could lead, however, to carbon starvation, reduced investment in pest defense and mortality on the longer term (Trugman *et al.*, 2018). Independent of the causality, such compensatory stimulation when comprising increased growth rates with larger xylem conduits can be a risk-taking strategy, making a tree more susceptible to reoccurring droughts.

Regardless of the actual recovery response, the earlier examples show that an antecedent drought can drive tree growth and

function in different directions and that current interpretations of the recovery process might not be straightforward. Opposite trajectories of recovery likely reflect a trade-off between a risk-minimizing acclimation strategy and the compensation of drought-induced limitations. Stressors such as drought events are known to induce persistent changes in trainable genes related to drought tolerance associated with a deep metabolic reprogramming (Ding *et al.*, 2012; Menezes-Silva *et al.*, 2017), which might be responsible for longer-term responses. Molecular stress memory is assumed to be conveyed by sustained alterations in levels of key signaling metabolites or transcription factors or by DNA methylation and histone modification (Crisp *et al.*, 2016). Only recently, two memory gene candidates have been identified, controlling in poplar trees physiological processes during drought stress, after recovery and during recurrent drought (Georgii *et al.*, 2019). During stress recovery, RNA metabolism, posttranscriptional gene silencing, and RNA-directed DNA methylation might be able to reset epigenetic and transcriptional modifications thus altering the memory over time making the plants 'forgetful' (Crisp *et al.*, 2016).

### Strategies for disentangling post-drought acclimation from impairment

Based on the earlier-mentioned considerations, we suggest that the current framework of recovery needs an amendment to include the acclimation potential of post-drought trajectories of functions. While we fully agree that the perturbation of a system is determined by the impact of an event and the recovery rate (Ingrisch & Bahn, 2018), post-drought trajectories might tell more about acclimation of trees. Fig. 1(a) shows the conceptual framework of our considerations, where slow retarded recovery could either indicate acclimation or continued impairment. In Fig. 1(b,c) we show the different hypothesized effects of repeated stress impact on tree function. In Fig. 1(b) we assume that retarded recovery conveys acclimation (compared to faster (i.e. 'normal') recovery or compensation) as indicated by a lower impact of the subsequent drought. Fig. 1(c) shows the trajectory of the alternative hypothesis with a stronger impact of a new drought during retarded recovery. If this framework is applied to tree ring analysis, which is often used to assess recovery retrospectively, lagged adjustments of growth may require new interpretation in the light of long-term acclimation. However, acclimation and risk avoidance might come with a reduction in biomass accumulation. If so, it would be difficult to disentangle such acclimation responses from negative growth legacies due to long-term impairment of plant functioning (which we recognize as an alternative reason for negative growth legacies).

A possibility for differentiation will be to assess if plants that did not fully 'recover' their growth after a first drought event are more or less resistant to a new drought compared to (1) control trees that have not been stressed before or (2) trees with a faster recovery trajectory (Fig. 1b,c). (1) Could be assessed in rain exclusion experiments simulating a single drought or repetitive drought periods over several years, followed by an opportunity for the trees to recover. Moreover, different drought intensities and frequencies could be simulated. During the recovery period, the previously

drought exposed plants and nonexposed controls need to be subjected to another drought event and then the impact of that drought event on tree functioning could be assessed. Moreover, long-term data series, e.g. on tree-ring width (Anderegg *et al.*, 2015) could be reassessed. Here the impact of drought events during the recovery phase could be compared with events occurring when no other drought affected the system several years before. Anderegg *et al.* (2015) also observed post-drought compensation of growth; one could test whether such compensation makes individuals more susceptible to new stress events during that overshooting period.





On the ecosystem level, Mitchell *et al.* (2016) give an example of a second drought event that occurs before the system has fully recovered from a first event; the second event increased the drought impact on stand gross primary productivity, thus supporting the scenario in Fig. 1(c). However, we need more long-term, large-scale datasets covering different forest ecosystems and tree species to quantitatively explore whether slow recovery can convey acclimation or not. Individual trees of the same species in the same stand can have different strategies concerning hydraulic safety (Hentschel *et al.*, 2014) and different provenances show different resilience towards drought events (Arend *et al.*, 2011; Jansen *et al.*, 2013). For (2) tree-ring series could be investigated for individual- or provenance-specific differences in recovery dynamics and screened for drought events that occur when part of the individuals or provenances have recovered while others have not yet, as shown in Fig. 1(b,c).

These ideas suggest a change in perspective as we evaluate drought responses. We suggest that some deviations from a steady-state may in fact be acclimative, reflecting the use of environmental information from stress events to adopt more conservative (or less conservative) functional traits, and to retain those traits for some finite period. Although the thresholds for response and the timing of the responses are likely to vary, recognition of their ability to enhance or avoid risk provides a means of considering the dynamics of risk management following a stress event.

### Author contributions

All authors have contributed to the development of the conceptual framework and to the writing of the manuscript.

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